Evolution of primate protomusicality via locomotion

David M. Schruth[1]
Christopher N. Templeton[2]
Darryl J. Holman[1]
Eric A. Smith[1]

1. University of Washington, Seattle, WA
2. Pacific University, Forest Grove, OR

***Abstract*:**

Animals communicate acoustically to report location and identity to conspecifics. More complex patterning of calls can also function as displays to potential mates and as territorial advertisement. Music and song are terms often reserved only for humans and birds, but elements of both forms of acoustic display are also found in non-human primates. While theories on proximate functions abound, ultimate drivers of specific call structures are less well understood. We hypothesized that spatio-temporal precision in landing during perilous arboreal locomotion favored the evolution of musical calling in early primates—vastly preceding the origin of more music-like behavior in hominoids and subsequent emergence of music in later hominids. We test this locomotion based hypothesis on the origins of proto-musicality using spectrographic depictions of vocal repertoires of modern day primates and corresponding estimates of locomotor activity. Phylogenetically controlled regression analysis of 54 primate species reveals that arboreal locomotion and monogamy are robust influences on complex calling patterns while controlling for other socioecological variables. Given that these findings rest primarily upon a handful of deep branching points in the primate tree, we conclude that this coevolution likely occurred very slowly, occupying on the order of tens of millions of years.

keywords: jumping, singing, signal, indicator, brachiation

Introduction

The origins of human music are confounded by a lack of consensus on theoretical evolutionary mechanisms and a seemingly unavoidable circularity in definitions (Schruth, Templeton and Holman, 2019a). Humans are complex musical beings with an unusual ability to adapt in cultural as well as genetic, cognitive, and ecological ways (Smith, 2011). Many correspondingly plausible adaptive mechanisms have been proposed including: sexual [or mate] choice (Darwin, 1871; Miller, 2000), "credible" signaling (Mehr *et al.*, 2020), coalitional or group selection (Hagen and Bryant, 2003), cultural evolution (Savage, 2019), gene-culture co-evolution (Cross, 2003), and epigenetic modification (Mehr *et al.*, 2020). Similarly unresolved are reasonable, albeit western (Jacoby *et al.*, 2020), definitions of the musical units of investigation including: song as "relatively complex" calls used in conspecific interactions (Beecher and Brenowitz, 2005), complex acoustic display (Templeton *et al.*, 2011), or learned complex calls (Fitch, 2015); music as information rich holistic patterns (Roederer, 1984), or creative orderly, organized, structured sequences with repeatable distinctive patterns (Marler, 2000); and musicality as a neurobiologically constrained and spontaneous capacity to receive and produce such stimuli (Morley, 2002, 2012; Honing *et al.*, 2015). A lack of clarity concerning the whats (outcomes and inputs) and hows (level, unit, tempo, and mode) of the evolution of musicality, however, has thus far prohibited rigorous testing of origins theories.

Akin to ambient noise obstructions of aquatic signals (Balebail and Sisneros, 2020), vegetative obstruction is thought to ecologically select for salient calls in arboreal animals (Morton, 1975; Krause, 1993; Slater, 2000). But human musicality presents a puzzle as we do not typically face similar constraints of arboreality, having adapted to more open habitats since the middle Pleistocene (Grove, 2011). While there are a multitude of (mostly arboreal) species who exhibit music-like behavior, humans are exceedingly singular in being strictly terrestrial (Brown and Jordania, 2013). These animals are known to use calls which contain song-like structures to localize themselves with conspecifics (Pollock, 1986; Catchpole and Slater, 1995). They have further compulsion towards more supererogatory vocal displays—ranging from asserting unique identity to specializing features of their territorial advertisements (Goustard, 1984; Pollock, 1986; Cooney and Cockburn, 1995). In the light of ecological resource instability (Mattison *et al.*, 2016) the case for musicality as a territorial signal in the most recent, hominid, environment of evolutionary adaptedness is debatable.

Plausible theories on music origins in humans range from infant attention (Trehub and Trainor, 1998; Dissanayake, 2000) to group communication (Brown, 2000; Hagen and Bryant, 2003). Darwin suggested that musical notes and rhythm functioned as part of courtship (Darwin, 1871), a theory others have endorsed (Miller, 2000; Dunbar, 2012). Until quite recently, the definition of music itself has historically been quite confounded with context, such as culture, materials, and group setting (Nettl, 2000), rendering any independent efforts to understand functional origins impossible (Schruth, Templeton and Holman, under review). And while it has been quite common to use the term *function* in a way that is nearly synonymous with *proximate context* (Pollock, 1986; Cooney and Cockburn, 1995; Templeton *et al.*, 2011; Mehr *et al.*, 2018), research into ultimate evolutionary influences is rare. We suggest that an investigation into these ultimate adaptive causes of hominid musicality could benefit from ecological and signaling theory insights on primate behavior whereby contexts are understood separately from the "acoustic features themselves" (Merriam and Merriam, 1964). To begin addressing the possible ecological drivers of a pre-hominid musicality, we examine vocalizations of extant primates and their possibly functional relationships with discontiguous locomotion through arboreal substrate. Specifically, we hypothesized that the bifurcating topologies of primates' arboreal habitats may not only have selected for the cognition necessary for *survival* in such precarious settings (Collins, 1921; Clark, 1959), but also that they may have favored the development of signals as indicators of these underlying abilities to conspecifics.

We leverage the overarching theoretical framework of behavioral ecology to model the fit of (e.g. musical) behavior to (e.g. an arboreal) environment—assuming a process of natural selection by both physical surroundings and the behavior of other organisms (Fox and Westneat, 2010). Additionally, we focus on the role of mate choice—the full cycle including courtship, copulation, fertilization, and parenting all recently acknowledged to represent a behavioral continuum (Dissanayake, 2008; Brooks *et al.*, 2010; Savage, 2019)—to help in resolving misunderstandings regarding which mating factors specifically are most important in shaping proto-musical behavior. We know, for example, that social monogamy is a strong predictor of musical behavior (Haimoff, 1986) but mechanistically why it evolved remains unclear (Mehr *et al.*, 2020). Accordingly, we propose a renewed focus upon natural selection on traits employed for both survival, via locomotion, *and* signaling behavior, via musical display.

We build on hypotheses that musical displays could demonstrate full maturation of generalized dimensional comparison abilities (Roederer, 1984) and [vocal-fold] motor control (Calvin, 1982; Roederer, 1982; Pinker, 1997)—capabilities useful for visual focus and other fine-motor tasks (Sacks, 2007). Beyond these proposed sensory-motor links, it is also possible that many auditory-musical spectrum behaviors are associated with spatial cognition (Dehaene *et al.*, 2003; Harris and Miniussi, 2003; Farrell *et al.*, 2012) such as auditory interval with verticality perception (Melara and O'Brien, 1987; Rusconi *et al.*, 2006; Bonetti and Costa, 2019). For the proto-musical calling of primates, we are most interested in correlates of melodic processing. Brain imaging studies typically locate music and melody perception in higher-cortical areas such as the temporal gyrus (Morley, 2002, 2012), but the limbic system has also recently been implicated (Harvey, 2017). These mid and hind brain areas, including the hippocampus, basal ganglia, and cerebellum, are thought to participate in melodic binding (Fernández, 2015). The hippocampus, in turn, also serves as a key facilitator of spatial cognition (Save and Poucet, 2000). Similar connections between song and equivalent brain structures in birds has also recently been observed (Nicholson, Roberts and Sober, 2018; Pidoux *et al.*, 2018). It is possible that these underlying spatial proficiencies, and corresponding spatio-sensory motor control abilities, could have been evolutionary selected in the *sender* to indirectly signal such qualities to conspecific receivers of musical calls. Senders and receivers could mutually benefit from the honesty of such signals via resource spacing, conflict avoidance, and mating potential. Dimensional precision for difficult aerial sensory-motor tasks (eg. landing with velocity in complex canopy habitats composed of tenuous branches) could efficiently be signaled to others within a breeding deme. This mode of signaling avoids venturing onto the forest floor or using diffused chemical, visually occluded, or otherwise ineffectual signals (Slater, 2000). In summary, we propose that arboreal primates, intent on avoiding terrestrial predation, frequently became at least moderately airborne in order to traverse gaps in substrate—and that the selection for corresponding (e.g. ocular) motor control and spatial cognition (e.g. resolving arbitrary branch shapes) for landing such bouts, maintained the honesty of such precise vocal signals.

The evidence for musical behavior in the archaeological record is slim (D'Errico *et al.*, 1998) and virtually non-existent in the paleontological record, making the testing of adaptive origins theories intractable. Alternatively, researchers might utilize modern day analogs to either reconstruct or statistically infer what ancestral calls may have been like (Wich and Nunn, 2002). Unfortunately, only a handful of primate species are considered "musical" (Geissmann, 2000) and such binary assessments make ancestral reconstruction statistically insoluble. In addition to traditional binary classifications, we used a continuous measure of proto-musicality, the acoustic reappearance diversity index [ARDI] (Schruth, Templeton and Holman, 2019c). ARDI is an estimate of the number of reappearing syllables within a call type (a rough proxy for protomusical behavior) and was derived from analysis of ethnomusicalogically prevalent acoustic features observed in primate calls (Schruth, Templeton and Holman, under review). We investigate this theory by analyzing non-human primate data within the evolutionary testing framework of phylogenetically controlled regression modeling.

Materials and Methods

We collected spectrographic vocal repertoires from the literature by searching Web of Science Citation Index (Garfield, 1970) using the search terms "spectro* AND primate* AND <genus>." Subsequent searches via google scholar (Acharya and Verstak, 2004) helped to fill in gaps by finding studies on species from genera with sparse representation in the larger dataset. In total 832 vocalizations from 60 species were collected corresponding to 39 genera and all but one primate family. Spectrograms were cropped out of their axes, renamed, and anonymized before scoring.

Scoring took place over the course of two days using bird call examples as training materials. Each of the five scorers had a different ordered spreadsheet of calls and scored, on a 0-10 scale, six different acoustic parameters: tone, interval, rhythm, repetition, transposition, and syllable count. Details of this scoring protocol are available online (Schruth, 2014). Scores were reliable across scorers with values ranging from 0.7 to 0.9 using Cronbach's alpha measure (Cronbach, 1970). These scores where then converted to a single number per vocalization via averaging between the scorers resulting in a total of 832 scores for six different parameters. This matrix was then input into PCA software (R Core Team, 2018) to help reduce the six variables into a more manageable number of variables for further analysis. PCA results suggested retaining (Jolliffe, 1972) repetition, transposition, and syllable count, the last of which is a commonly measured feature of avian songs (Wildenthal, 1965; Botero *et al.*, 2008). We reasoned that repetition and transposition are mutually exclusive and could be combined into a single measure of *redundancy.* Reappearance, in turn, was then multiplied by the unique syllable count to create a reappearance weighted measure of spectral shape diversity. This acoustic reappearance diversity index [ARDI] corresponded well to vocalizations designated by primary researchers as being "song" or "musical." Full details are only available in another manuscript (Schruth, Templeton and Holman, 2019b) but data and spectrograms are available online (Schruth, 2019).

Locomotion data was collated from the primate literature in a search procedure analogous to that used for the spectrographic data—using "locomot* primate* <genus>" search terms—as detailed above. In total the locomotion data set contained 54 different genera and 112 species. Studies were required at a minimum to have a quantitative estimate for leaping. But all other modes of locomotion were tabulated as well. Leaping and swinging percentages were cross-checked and verified against secondary compilations of locomotion (Rowe and Meyers, 2017). Leaping was coded as a composite variable combined with jump, air, and drop modes. Swinging was also composite with armswing and other suspensory modes.

We used regression (R Core Team, 2018) to compare our ARDI proto-musicality variable with a handful of candidate socioecological and locomotion variables. We used independent contrast (Felsenstein, 1985) values of each of these variables so as to control for non-independence of data collected from terminal nodes of the primate evolutionary tree, as closely related species shouldn't be considered independent points (Felsenstein, 1985). These regression results were further compared with PGLM (*caper* v. 0.5.2) regression (Orme *et al.*, 2013) on the same data using the same tree. We permuted over all possible modeling variable combinations—of *wooded*, *group size*, *monogamy*, as well as *leaping* and *swinging*—and averaged the resulting maximum likelihood estimates to obtain a static set of tree transformation parameters (kappa=2.5, lambda=0.2, delta=1.3) for the final PGLM analysis.

Results

Our results suggest that aerially discontiguous forms of locomotion, such as leaping and swinging, as well as social monogamy are each credibly associated with musical calling, but are somewhat contingent upon the specific method of phylogenetic control employed. Monogamy and locomotion contrasts exhibited the largest positive associations with protomusical calling as assessed by ARDI (Table 1, Figs 1 & 2). Monogamous species averaged nearly an entire additional reappearing syllable compared to non-monogamous species ($\beta \sim 1$; $p<0.03$). Leaping and swinging had nearly two fold greater effects than monogamy (for IC and PGLM respectively)—with an additional reappearing syllable in the most song-like call for every half range increase in leap bouts (IC; $\beta \sim 2$; $p<0.05$) and swing bouts (PGLM; $\beta \sim 2$; $p<0.02$). Further evidence of the importance of the monogamy and locomotion variables is seen in the fact that they were both significant under all models reported (Table 1) including the model with the highest R^2 and that with the lowest AIC (Table 2), although only simultaneously for both methods in the locomotion only model. Wooded habitat and group size had positive associations but were not significantly different from null. The locomotion and mating model with a relatively high explanation of variance (26% and 38%) and amongst the lowest AIC (155 and 138), respectively, is the most informative model for the purposes of this study. These results were even more striking, however, when the two locomotion measures were added together (PGLM; $\beta \sim 1.5$; $p<0.03$), while using a binary "musical" outcome variable (PGLM, $p<0.01$, for swing; IC, $p<0.02$, for leap), or under index compositions that included an even greater number of musical features, such as those incorporating both rhythm and tone.

Table 1. Multiple regression results for the contrasts between ARDI and various predictors

	locomotion		loco+mating		lowest AIC		[2nd] highest R²		full model	
wooded									0.15	(0.814)
group size							0.01	(0.053)	0.01	(0.516)
monogamy			0.93	(0.024) *	1.051	(0.007) **	0.98	(0.021) *	0.99	(0.022) *
leap	2.63	(0.003) **	1.81	(0.047) *	1.577	(0.064) .	1.97	(0.039) *	1.95	(0.043) *
swing	1.86	(0.098) .	0.89	(0.446)			0.97	(0.408)	0.96	(0.421)
R²	0.173	0.174	0.253	0.256	0.243	0.247	0.256	0.262	0.254	0.263
AIC	164.1	158.0	160.5	154.5	159.2	153.1	162.6	156.0	164.5	158.0

	locomotion		loco+mating		lowest AIC		[2nd] highest R²		full model	
wooded							0.49	(0.261)	0.40	(0.360)
group size							0.01	(0.323)	0.01	(0.256)
monogamy			0.65	(0.066) .	0.85	(0.006) **	0.94	(0.004) **	0.76	(0.040) *
leap	1.64	(0.022) *	0.82	(0.310)					0.85	(0.319)
swing	2.58	(<.001) ***	1.75	(0.013) *	1.4	(0.021) *	1.42	(0.021) *	1.79	(0.014) *
R²	0.322	0.337	0.366	0.380	0.355	0.368	0.377	0.391	0.386	0.403
AIC	145.2	139.7	143.4	138.0	142.4	137.1	144.4	139.1	145.5	140.0

This table of results includes multivariate regressions, full model (right) and all others (left), and reflect modeling based on the coefficient of determination (R^2) and Akaike's information criterion (AIC). The top and lower table correspond to independent contrasts and PGLM (using kappa=2.5, lambda=0.21, delta=1.33) regression methods respectively. P-values are contained within parenthesis with adjacent stars and periods indicating levels of significance (**=0.01, *=0.05, and .=0.1). The greater significance of leaping under PGLM and swinging under IC, likely stems from differences in how the underlying tree is allowed to transform and adjust (e.g. the ML optimized kappa, lambda, and delta) in compensating for the relative rarity of swinging primates.

Table 2. A list of tested statistical models and their corresponding AIC and R^2 values

best IC models by R2 and AIC	R²	AIC
ardi ~ monogamy + leap	0.247	153.1
ardi ~ monogamy + leap + swing	0.256	154.5
ardi ~ group + monogamy + leap	0.251	154.8
ardi ~ wood + monogamy + leap	0.247	155.1
ardi ~ group + monogamy + leap + swing	0.262	156.0
ardi ~ wood + monogamy + leap + swing	0.256	156.5
ardi ~ wood + group + monogamy + leap	0.253	156.7
ardi ~ wood + group + monogamy + leap + swing	0.263	158.0

Models were filtered by those with R^2 above 20% explained variance and sorted by increasing AIC.

best PGLM models by R2 and AIC	R²	AIC
ardi ~ monogamy + swing	0.365	137.1
ardi ~ monogamy + leap + swing	0.379	137.9
ardi ~ wood + monogamy + swing	0.376	138.2
ardi ~ group.size + monogamy + swing	0.372	138.5
ardi ~ group.size + monogamy + leap + swing	0.391	138.8
ardi ~ wood + group + monogamy + swing	0.388	139.1
ardi ~ wood + monogamy + leap + swing	0.385	139.4
ardi ~ leap + swing	0.335	139.6
ardi ~ wood + group + monogamy + leap + swing	0.401	139.9
ardi ~ group.size + leap + swing	0.340	141.2
ardi ~ wood + leap + swing	0.339	141.3

Fig 1. Plots of independent contrasts (between ARDI and two locomotion predictors) and the corresponding phylogenetic tree. Only a handful of ancient branching points in the primate tree drive these two significant correlations. Four of these divergences are between leaping species (stars at bottom) and two are from brachiating species (stars at top). With the exception of Platyrrhines, all of these key divergences match up quite well with species thought to be musical (black bands on right) by previous investigators (Geissmann, 2000). Branching point 69 is the deepest of these (at ~60 MYA) and happens to be the main split between Tarsiiformes and the rest of the Anthropoids. Branching point 87 and 100 are also rather old (~30 and ~20MYA), defining the split between Cercopithecoids and Hominoids, and Hylobatids from Hominids. Contrast #100 defines the significant difference between the hylobatids and hominoids who are split between brachiational arboreality and frequent knuckle-walking terrestriality. The rest of the main significance driving branching points (65, 64, and 63) all relate to splitting Indri and Galagoidae off from Pottos.

Fig 2. A scatterplot of reappearance diversity versus precision landing locomotion forms Precision limb landed forms of locomotion leaping and swinging are added together to comprise the total “aerial-spectrum” locomotion percentage and are plotted against max (±SE) reappearance diversity [ARDI] scores on primate spectrograms for each species (n=54). The standard error for each reappearance diversity score was estimated via bootstrap by taking the standard deviation of the max estimates for 10,000 different samplings (with replacement) of all vocalization-level reappearance diversity scores for each species. A smooth spline (gray line) was fit to the data (using 3 degrees of freedom). Point colors indicate taxonomic family membership as specified by the key. Pie chart rings around each point represents the swing and leap percentages as grey and black.

Discussion

The primary conclusion of our study—that arboreal pressures on primates may have driven the co-evolution of aerial spectrum locomotion (e.g. leaping and swinging) with song-like, proto-musical calling (Fig 2)—is largely derived from a handful of immoderate contrasts in each of these behaviors between phylogenetic neighbors (Fig 1). Specifically, the highly musical and frequently leaping Tarsiers and Indri (Fig 1: contrasts 72 and 67) and the quiet and non-leaping Loris and Aye-Aye (Fig 1: contrasts 68 and 66) constitute the four main drivers of the positive regression line trend in the leaping contrasts plot. More surprisingly, Galagos opposite Lorises (Fig 1: contrast 68) and Pitheciidae, such as titis, sakis, and uakaris, (opposite Atelidae, such as howler, spider, and woolly monkeys) emerge as relatively musical species as well (Fig 1: contrast 84).

The positive association between proto-musical calling and swinging is driven by two contrasts—that between gibbons and hominids and between apes and Old World monkeys (Fig 1: contrasts 106 and 90). This is understandable considering that there are nearly no other brachiating primates in the rest of the primate tree (Fig 1). Thus, although the significant positive association of swinging with musical calling observed here is contingent upon methodological assumptions, a more complete sampling of gibbon species will likely improve the resolution of this conditional association. Interestingly, the methodological discordance, that seems to only separately highlight these alternate forms of aerial locomotion, entirely disappears when the two mutually exclusive measures are simply added together (Fig 2).

Perhaps the most illustrative inverse-example to our origins scenario is the case of cheek-pouch monkeys (subfamily cercopithecinae) few of whom are musical, leapers, or monogamous (Rowe and Meyers, 2017). Evidently, in their transition to a strictly terrestrial existence, they lost all three of these traits. Only their hominoid relatives retained these traits long enough to find new adaptive functions as manifested in the swinging facilitated frugivory of socially monogamous lesser apes. While it likely required millions of years to fully unravel, the relatively recent radiation of these cercopithecines seems to have largely eroded the interdependent suite of arboreal specializations characteristic of their anthropoid progenitors.

Although the relationships we uncovered are robust under a number of different model compositions, they are admittedly largely driven by relatively few data-points—fewer than ten percent of the data drive the positive correlations. Furthermore, these contrasts correspond to branching times (Springer *et al.*, 2012) that average to well over ten million years old. It seems likely that this co-evolution is slow forming but could also decouple if one or the other trait was atrophied. Also, it seems that monogamy, shown to co-vary with ARDI previously (Schruth, Templeton and Holman, under review), could further play an interesting role as part of a three way co-evolution. Familial acquirement of such precarious locomotion strategies (e.g. group crossing of canopy-gaps) may not only forefend predation of kin, but could have so radicalized the evolution of arboreal ranging logistics, that *efficient signaling* of any congruent cognition might also have been incentivized.

This selective influence of precarious, time sensitive locomotion could apply to many other animals besides primates—songbirds, hummingbirds, cetaceans, bats, and arthropods all arguably could be considered to have proto-musical calls (McDermott, 2008; Hoeschele *et al.*, 2015), and all of whom either fly or swim. While the more aerial and terrestrial varieties above tend to land on thin terminal branches and slender grasses, the precise location of the surface for deep water diving mammals could have similarly unknown or otherwise challenging landing parameters. This could be particularly true for whales who feed on phytoplankton bloom driven food webs near polar ice sheets but must sometimes breath using polynyas. While it is known that species occupying habitats such as forest canopy or ocean depths use acoustic communication to efficiently overcome visual and olfactory obstructions (Slater, 2000), other forces are also likely at work as the calls of the orders listed above tend to go beyond just conveying location and identity. Mating (Darwin, 1871) and dominance (Hoeschele *et al.*, 2010), perhaps in combination, could have selected for even more complex and elaborate calling patterns. As mentioned, we believe that the uncertainty of secure landing conditions alone could have provided substantial selective pressures for the co-evolution at these protracted evolutionary rates.

As we have shown, in non-hominids, it is arboreality, and locomotion thereby, that appears to relate with musical calling. This pattern becomes complicated when considering our own genus which is much more terrestrial and musical than our semi-arboreal and less musical hominid cousins (gorillas, chimps, and orangutans). That is, our parallel proposal that a more human-like musicality accompanied the hominid shift to terrestriality runs counter to the trend of the rest of the primate order. How is it that three other genera of hominoid failed to inherit the likely arboreal and musical mating system that the hylobatids seemed to have retained through the Miocene? The relatively recent discovery of *Ardipithecus ramidus*, a putative singer (Clark and Henneberg, 2017), indicates that arboreal locomotion, in the form of above-branch palmigrade clambering, may have been practiced as recently as four million years ago (Lovejoy, 2009; Lovejoy *et al.*, 2009). Indeed, it is possible that this species (and presumably other Australopithecines) may have even slept in trees up until only a couple of million years ago (Fruth, Tagg and Stewart, 2018). It also appears terrestriality was something that evolved in parallel in multiple hominids (Larson, 1998; Lovejoy, 2009). Gorillas and chimps for example both became much more terrestrial and independently began knuckle walking millions of years after their divergence, perhaps due to increasingly dry conditions across the sub-continent (deMenocal, 2004).

So if an increase in terrestriality, and corresponding decrease in arboreality, primarily drives the *loss* of proto-musical calling, what is it about *Homo* that instead *promoted* musical behavior? It is possible that ballistics provides the answer. Accurate throwing (e.g. rocks, spears), the temporal reverse of catching (e.g. terminal branches) could pose similar selection pressures to aerial locomotion such as suspensory armswinging (Schruth, 2006). Humans throw things from great distance, with high momentum, and more accurately than any other species (Bingham, 1999). More generally however, tool use *is* known to be one of the primary defining characteristics of the genus Homo. The main evidence, dating back to Middle Paleolithic, abounds in the form of stone tool industries (Semaw *et al.*, 1997), which could have co-opted the Miocene adaptations of suspensory arm-swinging for associated precision hammering. Wooden spears, unlikely to preserve for many thousands of years, nevertheless show up at least more recently (Thieme, 1997). Thus, even if we are not certain about brachiation driving musical calling in hominoids, it is possible that precision arm swinging, or more fine-motor skills for tool-making, engendered a suite of neurological changes that overlapped with an increasingly complex musical calling. Hominid dominance over seasonal resources (e.g. herds of game) could be derived from analogous behaviors of hominoids (e.g. over fruiting terminal branches) tens of millions of years previously—and both may have acted as evolutionary inducers of salient acoustic displays sharply directed (Searcy and Beecher, 2009) towards conspecific resource competitors.

Singing requires micro-athletic mastery over fine muscles (Nettl, 1983; Sacks, 2007) in the vocal apparatus as well as memory to match previous acoustic gestures with current utterances and to plan future such gestures, as has been suggested previously (Roederer, 1984). Aside from fine distal *limb* motor control for grasp orientation adjustment, other possible skeletal-muscular candidates include breathing (Hewitt, MacLarnon and Jones, 2002) and *ocular* motor control—perhaps for late-locomotor-bout grasp placement adjustments. Subconscious pattern matching between disparate orbital inputs could modulate rectus muscle control of orbital position in the ocular cavity thereby enabling stereoscopic vision for such high-speed substrate encounters. Further possibilities of musical behavior serving as a (non-vision based) motor control signal include that for the fine muscles of the fingers perhaps for intricate tool making by hominins. It is further tempting to speculate that performance drumming aspects of *rhythmic* musicality could signal related precision butchering abilities (Jordania, 2008) to other long-distance scavenging parties of hominids dispersed across these more open and arboreally sparse settings.

Humans, by themselves, constitute nearly the entirety of the terrestrially musical creatures on earth, making a solution to the evolutionary puzzle so challenging—we represent only a minority, an extreme outlier datum, among hundreds of mostly non-terrestrial examples. There have been interesting explorations of understanding human music as derivative of more recent human adaptations such as rhythmic locomotion (Larsson, Richter and Ravignani, 2019) across earth's two-dimensional surface (Mithen, 2006) or in association with later-developing faculties such as language (Livingstone, 1973; Pinker, 1997) or dance (Hagen and Bryant, 2003). While a counter-argument regarding the possible confounding with language origins could be made, our built-in requirement for redundancy (in ARDI) makes scenarios invoking co-evolution with the far less repetitive, referentially linguistic forms of communication less compelling. Our results instead ought to inspire consideration of the tens of millions of preceding years of three-dimensional arboreality in anthropoids, suspensory armswinging in hominoids, and ballistics of hominids all of which likely eventually enabled re-terestrialzation (Ishida, 2006) and hunting of associated game (Calvin, 1983). A proposed transition from precision limb landing, on tenuous branches, followed by precision hammering upon thin blade faces, for forging tools, is strongly evidenced by the near-unanimous arboreal affinities of extinct and extant primates and the scores of archaeological sites documenting hominid lithic productivity. This historical sequence fortifies a continuous adaptive co-evolutionary scenario from the Paleocene to the late Pleistocene.

In sum, our findings regarding the potentially three-way coevolution between locomotion, monogamy, and proto-musicality suggest that the curious case of human music has deep primate roots. These roots plausibly derive from ancient patterns of subsistence based in precarious parabolic leaps, swings, and ballistic arches—all of which require last-minute fine-tuning adjustments in the wrist and fingers as well as high levels of coordination with the small muscles of the eye. Finally, if this arboreal, branch-dominance based locomotion evolved with more melodic calling, then a shift to terrestrial size-dominance may have instead engendered more deep-toned and perhaps group-conducive, rhythmic musciality (Merker, 1999). This two part evolution of more delicate melodic aspects first, followed by more rugged rhythmic aspects second, corresponding to our hominoid to hominid journey between two drastically different habitats, may help to better illuminate the enduring enigma and astonishing uniqueness of human music.

References Cited:

Acharya, A. and Verstak, A. (2004) *Google Scholar*. Available at: http://scholar.google.com.

Balebail, S. and Sisneros, J. A. (2020) ‘Relationship of advertisement call parameters with phenotypic traits in “singing” male plainfin midshipman’, *Integrative and Comparative Biology*, 60.

Beecher, M. and Brenowitz, E. (2005) ‘Functional aspects of song learning in songbirds’, *Trends in Ecology & Evolution*, 20(3), pp. 143–149. doi: 10.1016/j.tree.2005.01.004.

Bingham, P. M. (1999) ‘Human Uniqueness: A General Theory’, *The Quarterly Review of Biology*, 74(2), pp. 133–169. doi: 10.1086/393069.

Bonetti, L. and Costa, M. (2019) ‘Musical mode and visual-spatial cross-modal associations in infants and adults’, *Musicae Scientiae*, 23(1), pp. 50–68. doi: 10.1177/1029864917705001.

Botero, C. A. *et al*. (2008) ‘How Reliable are the Methods for Estimating Repertoire Size?’, *Ethology*, 114(12), pp. 1227–1238. doi: 10.1111/j.1439-0310.2008.01576.x.

Brooks, R. C. *et al*. (2010) ‘Mate Choice’, in *Evolutionary Behavioral Ecology*. New York: Oxford University Press.

Brown, S. (2000) ‘Evolutionary Models of Music: From Sexual Selection to Group Selection’, in Tonneau, F. and Thompson, N. S. (eds) *Perspectives in Ethology*. Boston, MA: Springer US, pp. 231–281. doi: 10.1007/978-1-4615-1221-9_9.

Brown, S. and Jordania, J. (2013) ‘Universals in the world’s musics’, *Psychology of Music*, 41(2), pp. 229–248.

Calvin, W. H. (1982) ‘Did Throwing Stones Shape Hominid Brain Evolution’, *Ethology and Sociobiology*, 3, pp. 115–124.

Calvin, W. H. (1983) ‘A Stone’s Throw and its Launch Window: Timing Precision and its Implications for Language and Hominid Brains’, *Journal of Theoretical Biology*, 104, pp. 121–135.

Catchpole, C. K. and Slater, P. J. B. (1995) *Bird Song: Biological Themes and Variation*. Cambridge, UK: Cambridge University Press.

Clark, G. and Henneberg, M. (2017) ‘Ardipithecus ramidus and the evolution of language and singing: An early origin for hominin vocal capability’, *HOMO*, 68(2), pp. 101–121. doi: 10.1016/j.jchb.2017.03.001.

Clark, W. (1959) *The Antecedents of Man*. Chicago: Quadrangle Books.

Collins, E. T. (1921) ‘Changes in the visual organs correlated with the adoption of arboreal life and with the assumption of the erect posture’, *Transactions of the Opithological Society*, 41, pp. 10–90.

Cooney, R. and Cockburn, A. (1995) ‘Territorial defense is the major function of female song in the superb fairy-wren, Malurus cyaneus’, *Animal Behaviour*, 49, pp. 1635–1647.

Cronbach, L. J. (1970) ‘Reliability (p. 161)’, in *Essentials of Psychological Testing*. Harper & Row.

Cross, I. (2003) 'Music as a biocultural phenomenon', *Neurosciences and Music*, 999, pp. 106–111.

Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. New York: Modern Library.

Dehaene, S. *et al*. (2003) 'Three parietal circuits for number processing', *Cognitive Neuropsychology*, 20, pp. 487–506.

deMenocal, P. B. (2004) 'African climate change and faunal evolution during the Pliocene–Pleistocene', *Earth and Planetary Science Letters*, 220(1–2), pp. 3–24. doi: 10.1016/S0012-821X(04)00003-2.

D'Errico, F. *et al*. (1998) 'A Middle Palaeolithic origin of music? Using cave-bear bone accumulations to assess the Divje Babe I bone "flute" (Neanderthal)', *Antiquity*, 72, pp. 65–79.

Dissanayake, E. (2000) 'Antecedents of the temporal arts in early mother-infant interaction', in Wallin, N. L., Merker, B., and Brown, S. (eds) *The Origins of Music*. Cambridge, Massachusetts: MIT Press, pp. 389–410.

Dissanayake, E. (2008) 'If music is the food of love, what about survival and reproductive success?', *Musicae Scientiae*, 12(1_suppl), pp. 169–195. doi: 10.1177/1029864908012001081.

Dunbar, R. I. M. (2012) 'On the evolutionary function of song and dance', in Bannan, N. (ed.) *Music, language, and human evolution*. Oxford University Press.

Farrell, T. M. *et al*. (2012) 'Song bout length is indicative of spatial learning in European starlings', *Behavioral Ecology*, 23, pp. 101–111. doi: 10.1093/beheco/arr162.

Felsenstein, J. (1985) 'Phylogenies and the Comparative Method', *The American Naturalist*, 125(1), pp. 1–15. doi: 10.1086/284325.

Fernández, I. A. (2015) *The role of the medial temporal lobe in binding lyrics and melodies□: a neuropsychological and neuroimaging approach*. Université Charles de Gaulle - Lille III.

Fitch, W. T. (2015) 'Four principles of bio-musicology', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1664), pp. 20140091–20140091. doi: 10.1098/rstb.2014.0091.

Fox, C. W. and Westneat, D. F. (2010) 'Adaptation', in Westneat, D. F. and Fox, C. W. (eds) *Evolutionary Behavioral Ecology*. New York: Oxford University Press.

Fruth, B., Tagg, N. and Stewart, F. (2018) 'Sleep and nesting behavior in primates: A review', *American Journal of Physical Anthropology*, 166(3), pp. 499–509. doi: 10.1002/ajpa.23373.

Garfield, E. (1970) 'Citation Indexing for Studying Science', *Nature*, 227(5259), pp. 669–671. doi: 10.1038/227669a0.

Geissmann, T. (2000) 'Gibbon songs and human music', in Wallin, N. L., Merker, B., and Brown, S. (eds) *The Origins of Music*. Cambridge, Massachusetts: MIT Press, pp. 103–123.

Goustard, M. (1984) 'Territorial Vocalizations in Adult Males of Free-Living Gibbons (Hylobates-Lar) Observed in Thailand', *Comptes Rendus De L Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences*, 298, pp. 65–67.

Grove, M. (2011) 'Change and variability in Plio-Pleistocene climates: modelling the hominin response', *Journal of Archaeological Science*, 38(11), pp. 3038–3047. doi: 10.1016/j.jas.2011.07.002.

Hagen, E. H. and Bryant, G. A. (2003) 'Music and dance as a coalition signaling system', *Human Nature-an Interdisciplinary Biosocial Perspective*, 14, pp. 21–51.

Haimoff, E. H. (1986) 'Convergence in the Duetting of Monogamous Old-World Primates', *Journal of Human Evolution*, 15, pp. 51–59.

Harris, I. M. and Miniussi, C. (2003) 'Parietal Lobe Contribution to Mental Rotation Demonstrated with rTMS', *Journal of Cognitive Neuroscience*, 15(3), pp. 315–323. doi: 10.1162/089892903321593054.

Harvey, A. R. (2017) 'How the Brain Processes Music', in *Music, Evolution, and the Harmony of Souls*. Oxford University Press.

Hewitt, G., MacLarnon, A. and Jones, K. E. (2002) 'The Functions of Laryngeal Air Sacs in Primates: A New Hypothesis', *Folia Primatologica*, 73(2–3), pp. 70–94. doi: 10.1159/000064786.

Hoeschele, M. *et al.* (2010) 'Dominance signalled in an acoustic ornament', *Animal Behaviour*, 79(3), pp. 657–664. doi: 10.1016/j.anbehav.2009.12.015.

Hoeschele, M. *et al.* (2015) 'Searching for the origins of musicality across species', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1664), p. 20140094. doi: 10.1098/rstb.2014.0094.

Honing, H. *et al.* (2015) 'Without it no music: cognition, biology and evolution of musicality', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1664), p. 20140088. doi: 10.1098/rstb.2014.0088.

Ishida, H. (2006) 'Current Thoughts on Terrestrialization in African Apes and the Origin of Human Bipedalism', in Ishida, H. et al. (eds) *Human Origins and Environmental Backgrounds*. Springer US (Developments in Primatology: Progress and Prospects), pp. 259–266. doi: 10.1007/0-387-29798-7_20.

Jacoby, N. *et al.* (2020) 'Cross-Cultural Work in Music Cognition: Challenges, Insights, and Recommendations', *Music Perception: An Interdisciplinary Journal*, 37(3), pp. 185–195. doi: 10.1525/mp.2020.37.3.185.

Jolliffe, I. T. (1972) 'Discarding variables in a Principal Component Analysis: Artificial Data', *Royal Statistical Society*, 21(2), pp. 160–173.

Jordania, J. (2008) 'Origins of rhythm and the defence strategy of human ancestors', in Tsurtsumia, R. (ed.) *Problems of Traditional Polyphony. Materials of the Third International Symposium on Traditional Polyphony. Third International Research Centre of Traditional Polyphony*, Tbilisi State Conservatory, pp. 55–66.

Krause, B. (1993) 'The niche hypothesis: a virtual symphony of animal sounds, the origins of musical expression and the health of habitats', *The Soundscape Newsletter*.

Larson, S. G. (1998) ‘Parallel evolution in the hominoid trunk and forelimb’, *Evolutionary Anthropology: Issues, News, and Reviews*, 6(3), pp. 87–99. doi: 10.1002/(SICI)1520-6505(1998)6:3<87::AID-EVAN3>3.0.CO;2-T.

Larsson, M., Richter, J. and Ravignani, A. (2019) ‘Bipedal Steps in the Development of Rhythmic Behavior in Humans’, *Music & Science*, 2, p. 205920431989261. doi: 10.1177/2059204319892617.

Livingstone, F. B. (1973) ‘Did the Australopithecines Sing?’, *Current Anthropology*, 14(1/2), pp. 25–29. doi: 10.1086/201402.

Lovejoy, C. O. (2009) ‘Reexamining Human Origins in Light of Ardipithecus ramidus’, *Science*, 326(5949), pp. 74–74, 74e1-74e8. doi: 10.1126/science.1175834.

Lovejoy, C. O. *et al.* (2009) ‘The Great Divides: Ardipithecus ramidus Reveals the Postcrania of Our Last Common Ancestors with African Apes’, *Science*, 326(5949), pp. 73–73, 100–106. doi: 10.1126/science.1175833.

Marler, P. (2000) ‘Origins of music and speech: insights from animals’, in Wallin, N. L., Merker, B., and Brown, S. (eds) *The Origins of Music*. Cambridge, Massachusetts: MIT Press, pp. 31–48.

Mattison, S. M. *et al.* (2016) ‘The evolution of inequality: The Evolution of Inequality’, *Evolutionary Anthropology: Issues, News, and Reviews*, 25(4), pp. 184–199. doi: 10.1002/evan.21491.

McDermott, J. (2008) ‘The evolution of music’, *Nature*, 453, pp. 287–288. doi: Editorial Material.

Mehr, S. A. *et al.* (2018) ‘Form and Function in Human Song’, *Current Biology*, 28(3), pp. 356-368.e5. doi: 10.1016/j.cub.2017.12.042.

Mehr, S. A. *et al.* (2020) ‘Origins of music in credible signaling’, *Behavioral and Brain Sciences*, (target article).

Melara, R. D. and O’Brien, T. P. (1987) ‘Interaction between synesthetically corresponding dimensions.’, *Journal of Experimental Psychology: General*, 116(4), pp. 323–336. doi: 10.1037/0096-3445.116.4.323.

Merker, B. (1999) ‘Synchronous chorusing and the origins of music’, *Musicae Scientiae*, pp. 59–73.

Merriam, A. and Merriam, V. (1964) *The Anthropology of Music*. Northwestern University Press.

Miller, G. F. (2000) ‘Evolution of Human Music through Sexual Selection’, in *The Origins of Music*. Cambridge, Massachusetts: MIT Press, pp. 328–360.

Mithen, S. (2006) *The Singing Neanderthals*. Cambridge, MA: Harvard University Press.

Morley, I. (2002) ‘Evolution of the physiological and neurological capacities for music’, *Cambridge Archaeological Journal*, 12, pp. 195–216.

Morley, I. (2012) ‘Hominin physiological evolution and the emergence of musical capacities’, in Bannan, N. (ed.) *Music, Language, and Human Evolution*. Oxford University Press.

Morton, E. S. (1975) ‘Ecological sources of selection on avian sounds’, *The American Naturalist*, 109(965), pp. 17–34.

Nettl, B. (1983) *The Study of Ethnomusicology*. Chicago: University of Illinois Press.

Nettl, B. (2000) ‘An Ethnomusicologist Contemplates Musical Universals’, in *The Origins of Music*. Cambridge, Massachusetts: MIT Press, pp. 463–472.

Nicholson, D. A., Roberts, T. F. and Sober, S. J. (2018) ‘Thalamostriatal and cerebellothalamic pathways in a songbird, the Bengalese finch’, *Journal of Comparative Neurology*, 526(9), pp. 1550–1570. doi: 10.1002/cne.24428.

Orme, D. *et al*. (2013) *The caper package: comparative analysis of phylogenetics and evolution in R*.

Pidoux, L. *et al*. (2018) ‘A subcortical circuit linking the cerebellum to the basal ganglia engaged in vocal learning’, *eLife*, 7, p. e32167. doi: 10.7554/eLife.32167.

Pinker, S. (1997) *How the Mind Works*. New York: W.W. Norton & Company.

Pollock, J. I. (1986) ‘The song of the Indris: natural history form and function’, *International Journal of Primatology*, 7, p. 225.

R Core Team (2018) *R: A Language and Environment for Statistical Computing*. Vienna, Austria. Available at: https://www.R-project.org/.

Roederer, J. G. (1982) ‘Physical and Neuropsychological Foundations of Music’, in Clynes, M. (ed.) *Music, Mind, and Brain*. Boston, MA: Springer US, pp. 37–46. doi: 10.1007/978-1-4684-8917-0_3.

Roederer, J. G. (1984) ‘The Search for a Survival Value of Music’, *Music Perception*, 1, pp. 350–356.

Rowe, N. and Meyers, M. (2017) *All the World’s Primates*. Charlestown, RI: Pogonias Press.

Rusconi, E. *et al*. (2006) ‘Spatial representation of pitch height: the SMARC effect’, *Cognition*, 99(2), pp. 113–129. doi: 10.1016/j.cognition.2005.01.004.

Sacks, O. (2007) ‘Atheletes of the small muscles: musician’s dystonia’, in *Musicophilia*. New York: Vintage Books.

Savage, P. E. (2019) ‘Cultural evolution of music’, *Palgrave Communications*, 5(1). doi: 10.1057/s41599-019-0221-1.

Save, E. and Poucet, B. (2000) ‘Hippocampal□parietal cortical interactions in spatial cognition’, *Hippocampus*, 10(4), p. 491. doi: 10.1002/1098-1063(2000)10:4<491::AID-HIPO16>3.0.CO;2-0.

Schruth, D. M. (2006) *Melodic Display as an Honest Signal of Remote Targeting Ability: A Meta-Analysis of the Correlated Evolution of Locomotion and Vocalizations in Primates*. Masters Thesis. University of Washington.

Schruth, D. M. (2014) 'Protocol for scoring animal calls on structural acoustic features prevalent in human music', *Protocols.io*. doi: 10.17504/protocols.io.bp5emq3e.

Schruth, D. M. (2019) *Structural acoustic features of human musicality scored on primate vocalizations*. Available at: https://osf.io/bvsfz/.

Schruth, D. M., Templeton, C. N. and Holman, D. J. (under review) 'On reappearance and complexity in musical calling', *PLoS ONE*.

Schruth, D. M., Templeton, C. N. and Holman, D. J. (2019a) 'A definition of song, using human music universals observed in primate calls', *BioRxiv*. doi: 10.1101/649459.

Schruth, D. M., Templeton, C. N. and Holman, D. J. (2019c) 'Acoustic reappearance diversity: quantifying musicality in primate vocalizations', in *American Association of Physical Anthropologists*. *88th Annual Meeting*, Cleveland, OH: American Journal of Physical Anthropology. doi: 10.1002/ajpa.23802.

Searcy, W. A. and Beecher, M. D. (2009) 'Song as an aggressive signal in songbirds', *Animal Behaviour*, 78(6), pp. 1281–1292. doi: 10.1016/j.anbehav.2009.08.011.

Semaw, S. *et al.* (1997) '2.5-million-year-old stone tools from Gona, Ethiopia', *Nature*, 385(6614), pp. 333–336. doi: 10.1038/385333a0.

Slater, P. J. B. (2000) 'Birdsong Repertoires: Their Origins and Use', in *The Origins of Music*. Cambridge, Massachusetts: MIT Press, pp. 49–63.

Smith, E. A. (2011) 'Endless forms: human behavioural diversity and evolved universals', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1563), pp. 325–332. doi: 10.1098/rstb.2010.0233.

Springer, M. S. *et al.* (2012) 'Macroevolutionary Dynamics and Historical Biogeography of Primate Diversification Inferred from a Species Supermatrix', *PLoS ONE*. Edited by R. Stanyon, 7(11), p. e49521. doi: 10.1371/journal.pone.0049521.

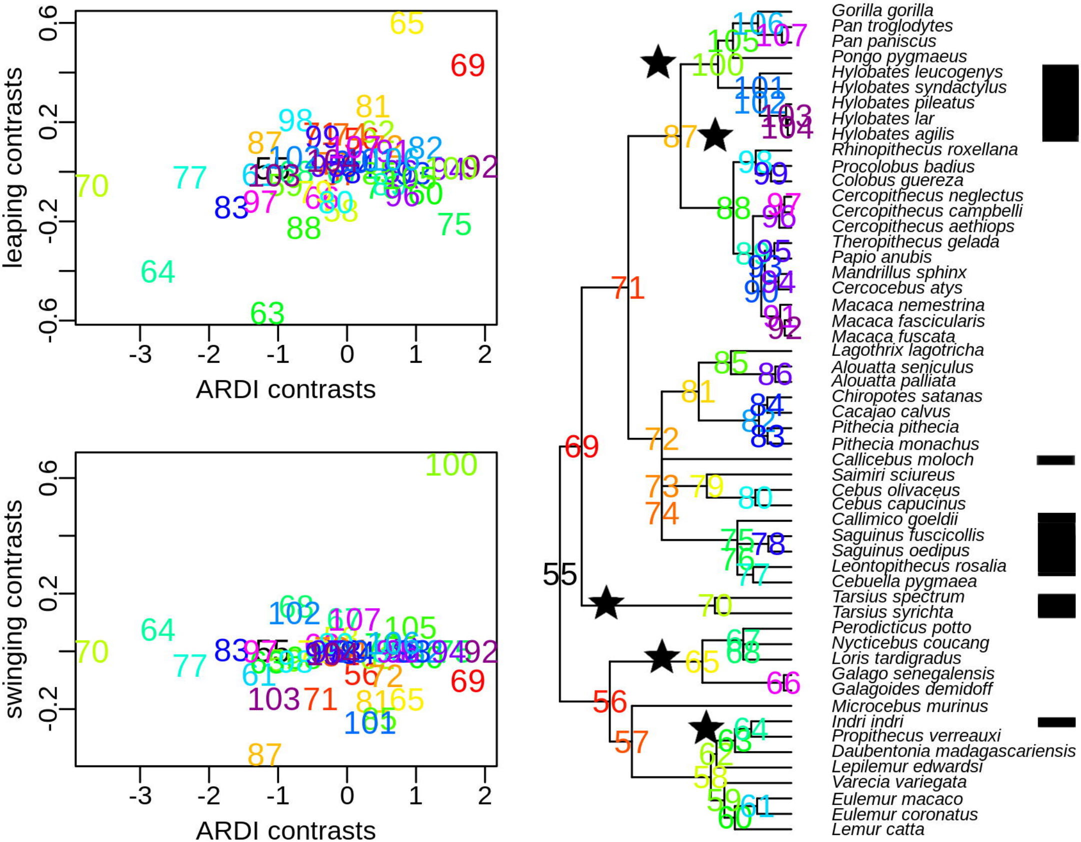
Templeton, C. N. *et al.* (2011) 'Song duets function primarily as cooperative displays in pairs of happy wrens', *Animal Behaviour*, 82, pp. 1399–1407. doi: Article.

Thieme, H. (1997) 'Lower Palaeolithic hunting spears from Germany', *Nature*, 385(6619), pp. 807–810. doi: 10.1038/385807a0.

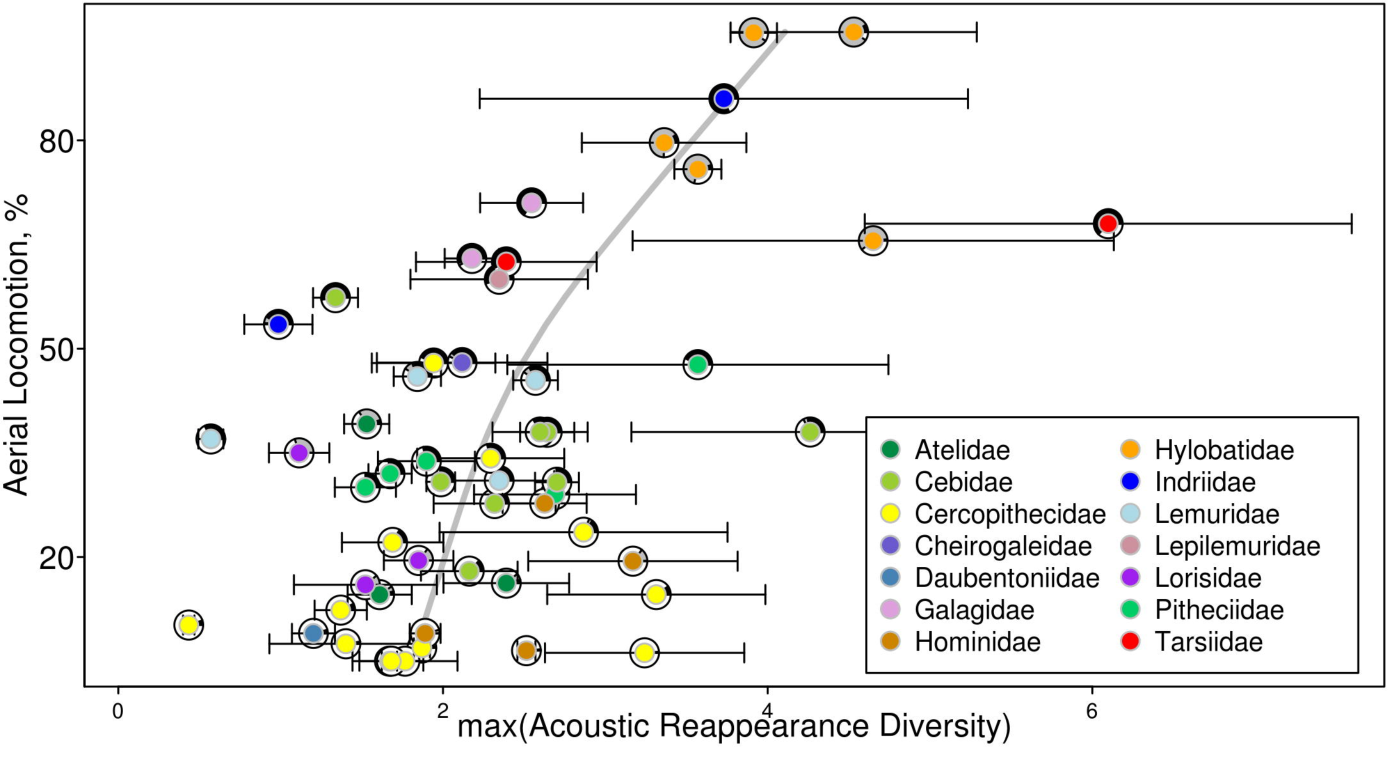
Trehub, S. E. and Trainor, L. (1998) 'Singing to infants: Lullabies and play songs', in *Advance Infancy Research*, pp. 43–78.

Wich, S. A. and Nunn, C. (2002) 'Do male "long distance calls" function in mate defense? A comparative study of long-distance calls in primates', *Behavioral Ecology and Sociobiology*, 52, pp. 474–484.

Wildenthal, J. L. (1965) 'Structure in Primary Song of the Mockingbird (Mimus polyglottos)', *The Auk*, 82(2), pp. 161–189. doi: 10.2307/4082931.



leaping contrasts
ARDI contrasts
swinging contrasts
ARDI contrasts
Gorilla gorilla
Pan troglodytes
Pan paniscus
Pongo pygmaeus
Hylobates leucogenys
Hylobates syndactylus
Hylobates pileatus
Hylobates lar
Hylobates agilis
Rhinopithecus roxellana
Procolobus badius
Colobus guereza
Cercopithecus neglectus
Cercopithecus campbelli
Cercopithecus aethiops
Theropithecus gelada
Papio anubis
Mandrillus sphinx
Cercocebus atys
Macaca nemestrina
Macaca fascicularis
Macaca fuscata
Lagothrix lagotricha
Alouatta seniculus
Alouatta palliata
Chiropotes satanas
Cacajao calvus
Pithecia pithecia
Pithecia monachus
Callicebus moloch
Saimiri sciureus
Cebus olivaceus
Cebus capucinus
Callimico goeldii
Saguinus fuscicollis
Saguinus oedipus
Leontopithecus rosalia
Cebuella pygmaea
Tarsius spectrum
Tarsius syrichta
Perodicticus potto
Nycticebus coucang
Loris tardigradus
Galago senegalensis
Galagoides demidoff
Microcebus murinus
Indri indri
Propithecus verreauxi
Daubentonia madagascariensis
Lepilemur edwardsi
Varecia variegata
Eulemur macaco
Eulemur coronatus
Lemur catta



Aerial Locomotion, %
80
50
20
0
2
4
6
max(Acoustic Reappearance Diversity)
Atelidae
Cebidae
Cercopithecidae
Cheirogaleidae
Daubentoniidae
Galagidae
Hominidae
Hylobatidae
Indriidae
Lemuridae
Lepilemuridae
Lorisidae
Pitheciidae
Tarsiidae